Seedling Resistance to Tan Spot and Stagonospora Nodorum Blotch in Synthetic Hexaploid Wheats

S. S. Xu,* T. L. Friesen, and A. Mujeeb-Kazi

ABSTRACT

Tan spot and Stagonospora nodorum blotch (SNB), caused by fungi *Pyrenophora tritici-repentis* (Died.) Drechs. [anamorph: *Drechslera tritici-repentis* (Died.) Shoem.] and *Phaeosphaeria nodorum* (E. Müller) Hedjaroude [anamorph: *Stagonospora nodorum* (Berk.) Castellani & Germano], respectively, are two important foliar diseases of wheat (*Triticum aestivum* L.). The objective of this study was to evaluate the two sets of elite synthetic hexaploid wheat (SHW, $2n = 6x = 42$, AABBDD) lines (Elite 1 and Elite 2) developed at the International Maize and Wheat Improvement Center (CIMMYT) for their seedling resistance to *P. tritici-repentis* and *P. nodorum*. In this study, 120 elite CIMMYT SHW lines and their durum wheat [*T. turgidum* subsp. *durum* (Desf.) Husn.] parents were inoculated with *P. tritici-repentis* race 1 and a standard field isolate (Sn2000) of *P. nodorum*, respectively, in two separate three-replication experiments. The seedling reactions to *P. tritici-repentis* and *P. nodorum* were evaluated 7 and 10 d postinoculation, respectively. The plant leaves were also infiltrated with the host-selective toxin (HST) Ptr ToxA at the two-leaf stage and sensitivity was evaluated 3 to 4 d postinfiltration. As expected, most SHW lines were the same as their durum parents in their sensitivity to Ptr ToxA because the sensitivity locus *Tsn1* is located on chromosome 5B. However, a few of the synthetics were different from their durum parents, suggesting that heterozygosity and heterogeneity might exist in some of the SHW lines and durum parents. The toxin sensitivity significantly increased susceptibility of the synthetics to tan spot but had no significant effects on durum parents. The data showed that 56 (46.7%) and 36 (30.0%) SHW lines were resistant to tan spot and SNB, respectively, whereas resistance was almost absent in the durum parents. These results suggest that the elite CIMMYT synthetics are an excellent source of resistance to tan spot and SNB and should be useful in developing new resistant cultivars and adapted germplasm in bread wheat.

Synthetic hexaploid wheat (SHW) ($2n = 6x = 42$, AABBDD), which is the colchicine-induced amphiploid produced from the hybrid between tetraploid wheat (*T. turgidum* L., $2n = 4x = 28$, AABB) and *Aegilops tauschii* Coss. ($2n = 2x = 14$, DD), is a useful bridging germplasm for the introgression of desirable genes from *A. tauschii* to bread wheat (*T. aestivum* L.). Since the first synthesized hexaploid wheat was produced in the 1940s (McFadden and Sears, 1944), numerous synthetics have been developed and some have been used to transfer desirable traits from *A. tauschii* to common wheat, such as resistance to leaf rust (*Puccinia triticina* Eriks.), Septoria tritici blotch (*Septoria tritici* Roberge in Desmaz.), Karnal bunt (*Tilletia indica* Mitra), and wheat curl mite (*Eriophyes tulipae* Keifer) (Reviewed by Cox, 1998). Because of a large degree of genetic variation compared with bread wheat, synthetics are good materials for developing mapping populations such as recombinant inbred lines and doubled haploids. The International Triticeae Mapping Initiative mapping population developed from the cross between the CIMMYT SHW line W-7984 and the hard red spring wheat (HRSW) 'Opata 85' has been extensively used for mapping the wheat genome.

Tan spot and SNB are important foliar diseases of bread wheat and durum wheat, and have the ability to cause serious yield losses. Tan spot has been reported to cause yield losses ranging from 3 to 50% (Rees and Platz, 1983; Riede et al., 1996) and yield losses by SNB can be as high as 50% (Fried and Meister, 1987; King et al., 1983). It was also recorded that *P. nodorum* can affect grain quality such as milling and baking quality (Mckendry et al., 1995). In addition, both *P. tritici-repentis* and *P. nodorum* produce certain HSTs. The toxins Ptr ToxA (Ciuffetti and Tuori, 1999) and SnTox1 (Liu et al., 2003) are produced by *P. tritici-repentis* race 2 and *P. nodorum* isolate Sn2000, respectively. Sensitive wheat genotypes to Ptr ToxA and SnTox1 are usually associated with susceptibility to each of the diseases (Friesen et al., 2003a; Liu et al., 2003).

In North Dakota and nearby states, incidences of tan spot and SNB are becoming more common in recent years. However, the majority of current bread and durum wheat cultivars in the region are susceptible. Rees and Platz (1990) evaluated 1400 bread wheat lines for their resistance to *P. tritici-repentis* and no complete resistance was found. Riede et al. (1996) identified several hexaploid wheat genotypes with good levels of resistance to tan spot from a collection of HRSW cultivars and germplasm from Brazil and seven synthetics. Similar to tan spot, complete resistance or immunity to SNB has not been identified in durum and bread wheat, but various levels of partial resistance were identified in wheat and related species (Eyal, 1999). Because Fusarium head blight (FHB; *Fusarium graminearum* Schwabe) is still the priority problem in current wheat breeding and genetic research programs in the major wheat production regions in the USA, studies on identification and utilization of new sources of resistance to tan spot and SNB have been neglected. This situation poses a potential threat to wheat production. Therefore, there is a need to find new

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Abbreviations: CIMMYT, International Maize and Wheat Improvement Center; FHB, Fuarium head blight; HRSW, hard red spring wheat; HST, host-selective toxin; PDA, potato dextrose agar; SHW, synthetic hexaploid wheat; SNB, Stagonospora nodorum blotch; WGRC, Wheat Genetics Resource Center.

sources of high level resistance to tan spot and SNB and transfer the resistance to local cultivars and adapted germplasm. Here we report the evaluation of elite CIMMYT synthetics and their durum wheat parents for seedling reactions to *P. tritici-repentis*, Ptr ToxA, and *P. nodorum*.

MATERIALS AND METHODS

Plant Materials

Mujeeb-Kazi et al. (2000) and Mujeeb-Kazi and Delgado (2001) selected two sets (Elite 1 and Elite 2) of elite synthetics and reported a list of characterized traits. In the USA, the Wheat Genetics Resource Center (WGRC) at Kansas State University in Manhattan, KS, is the repository of these elite sets of synthetics. This secondary WGRC distribution site of the CIMMYT SHW germplasms serves a rapid means to provide the germplasms to the researchers in the USA and Canada. The original seeds of the synthetics and their durum parents used in this study were kindly provided by Bikram S. Gill and Jon Raupp at the WGRC.

A total of 155 entries, including 87 lines of Elite 1, all 33 lines of Elite 2, and 35 lines of durum wheat parents, were used in this study. The TA and line number at the WGRC and pedigrees are listed in Table 1. The entries in Table 1 are divided into 36 groups based on the durum wheat parent. The groups are alphabetically ordered and the first entry in each group is the durum wheat, followed by the synthetics. The durum wheat SKARV 2 for SHW line 4153-11 (Entry 110) was not available. The CIMMYT SHW line W-7976 (Entry 156) and the HRSW line ND495 (Entry 157) developed at North Dakota State University were used as the resistant and susceptible checks, respectively.

Evaluation of Reactions to *Pyrenophora tritici-repentis* and Ptr ToxA

Evaluation of reactions to *P. tritici-repentis* and Ptr ToxA was conducted under controlled greenhouse and growth chamber conditions using similar experimental procedures described by Friesen et al. (2003b) and Riede et al. (1996). The original seeds received from the WGRC were pregerminated in Petri dishes and the germinated seeds were then planted in super-cell cones (Stuewe and Sons, Inc., Corvallis, OR) with Sunshine Mix fertilized with Osmocote Plus 15–19–12 (N–P–K; Scotts Sierra Horticultural Product Company, Marysville, OH). Two to three plants were planted in each cone. Each genotype was planted in three cones in each of three replications. Because of their poor germination, durum wheats 'Arlequin 1' (Entry 17), 'Croc 1' (Entry 44), LCK59.61 (Entry 96), 'Yar' (Entry 127), and YAV 2/TEZ (Entry 133) were planted only in two replications, and 'Dverd 2' (Entry 79) was planted only in one replication (Table 1). The cones were placed in RL98 trays (Stuewe and Sons, Inc., Corvallis, OR) and the seeds of susceptible check ND495 were planted in all the cones around the borders on the RL98 trays except for three cones planted with the resistant check.

At the two-leaf stage, plant leaves (three plants per line) were infiltrated with purified Ptr ToxA, which was provided by S.W. Meinhardt, Department of Biochemistry, North Dakota State University, Fargo, ND. The toxin was originally purified from *P. tritici-repentis* race 2 (isolate 86-124) as described by Zhang et al. (1997). When the secondary leaf was fully expanded, it was assayed by infiltrating approximately 25 μL of partially purified toxin (10 μg mL^{-1}) using a 1-mL syringe with the needle removed. The boundaries of the infiltration sites were marked with a nontoxic felt pen before water-soaking disappeared. After infiltration, all plants were moved to a growth chamber at 21°C with a 12-h photoperiod. Leaves were evaluated 3 to 4 d after infiltration and scored as insensitive (−) or sensitive (+).

After evaluation of sensitivity, all the plants were inoculated with *P. tritici-repentis* race 1 conidia. *Pyrenophora tritici-repentis* race 1 was chosen because of its prevalence in North America (Ali and Francl, 2003). Race 1 also contains the virulence factors found in race 2 (Lamari et al., 2003), the second most prevalent race found in the field (Ali and Francl, 2003). The race 1 isolate Pti2 was obtained from a wheat field in South Dakota. For preparation of inoculum, the mycelial plugs from a parental colony grown on Potato Dextrose Agar (PDA) or V8-PDA [150 mL V8 juice (Campbell Soup Company, Camden, NJ), 10 g PDA, 3 g $CaCo_3$, 10 g agar, and 850 mL distilled water] were placed on V8-PDA plates and incubated in the dark for 5 to 6 d at 20°C. After flooding the plates with sterile distilled water, the plates were incubated under florescent light for 24 h at 20 to 22°C followed by 18 to 24 h under dark at 16°C. The conidial inoculum suspensions were produced by washing plates with sterile distilled water and scraping the spores from the plate. The concentration was further adjusted to 3000 spores mL^{-1}. Plants were inoculated until runoff with a handheld sprayer.

Following inoculation, plants were placed into a humidity chamber at 21°C with 100% relative humidity for 24 h. After the humidity period, plants were held in a growth chamber at 21°C in a 12 h photoperiod for the remainder of the experiment. Plants were evaluated 7 d postinoculation. The disease was scored on a 1-to-5 scale lesion-type rating system developed by Lamari and Bernier (1989), with 1 being resistant, 2 moderately resistant, 3 moderately resistant or moderately susceptible, 4 susceptible, and 5 highly susceptible. Lines showing equal number of two lesion types were given an intermediate reaction type (e.g., Reaction Type 1 and 2 equals 1.5).

Evaluation of Reactions to *Phaeosphaeria nodorum*

After evaluation of reactions to *P. tritici-repentis*, all the plants were transplanted into 15-cm clay pots in the greenhouse for seed increase. Before flowering, the majority of the spikes were bagged, and self-pollinated seeds were further used for evaluation of seedling resistance to *P. nodorum*. The standard *P. nodorum* field isolate Sn2000 was used for inoculating the plants at the two- to three-leaf stage. Sn2000 was collected from a North Dakota wheat field in 1980 and was chosen because it has been used to screen North Dakota germplasm and breeding lines and has been shown to be an aggressive isolate that produces the newly discovered HST SnTox1 (Liu et al., 2003).

Isolate Sn2000 was grown by streaking 200 μL of pycnidial spores onto V8-PDA. Cultures were then grown for 7 to 10 d and inoculum was obtained by washing the plates with sterile distilled water and adjusting concentration to 1×10^6 conidia mL^{-1}. The inoculation was conducted using the same procedure as described for *P. tritici-repentis*. The plants were evaluated for reaction to the fungus 10 d postinoculation. The rating system used for *P. nodorum* was also a qualitative numerical scale based on lesion type using the tan spot rating scale as a guide (Lamari and Bernier 1989). Reaction Type 1 consists of few penetration points with small necrotic and/or dark spots (resistant) (Fig. 1a); Type 2 consists of lesions with dark spots and little surrounding necrosis or chlorosis (moderately resistant) (Fig. 1b); Type 3 has dark lesions completely surrounded by necrosis or chlorosis, lesions 2 to 3 mm in size (moderately susceptible) (Fig. 1c); Type 4 consists of larger necrotic or chlorotic lesions 4 mm or greater with little coalescence (suscepti-

Table 1. Seedling reactions of elite CIMMYT synthetic hexaploid wheats to *Pyrenophora tritici-repentis* (Ptr) and *Phaeosphaeria nodorum*.

Entry No.†	TA-Line‡	Pedigree	Reaction to ToxA§	Reaction to Ptr		Reaction to *P. nodorum*		
				AVG¶	SD	FLECK#	AVG	SD
1	4154-49	Aconchi 89	−	3.67	1.04	−	4.33	0.76
2	4152-26	Aconchi 89/*A. tauschii* (309)††	−	1.00*	0.00	+	1.83*	0.58
3	4154-4	Altar 84	−	3.00	0.50	−	3.83	0.58
4	4152-1	Altar 84/*A. tauschii* (188)	−	1.00*	0.00	+	1.17**	0.29
5	4152-3	Altar 84/*A. tauschii* [TA 1651] (192)	−	1.17**	0.29	+	1.50*	0.00
6	4152-4	Altar 84/*A. tauschii* (193)	−	1.50*	0.00	+	2.83	1.04
7	4152-5	Altar 84/*A. tauschii* (198)	−	1.50*	0.00	+	1.50*	0.00
8	4152-7	Altar 84/*A. tauschii* (205)	−	1.17**	0.29	+	1.50*	0.00
9	4152-9	Altar 84/*A. tauschii* (211)	−	1.00*	0.00	+	1.33**	0.29
10	4152-16	Altar 84/*A. tauschii* (219)	−	1.33*	0.29	+	1.67*	0.29
11	4152-20	Altar 84/*A. tauschii* (221)	−	1.00*	0.00	+	1.33**	0.29
12	4152-25	Altar 84/*A. tauschii* (224)	−	1.00*	0.00	+	1.33**	0.29
13	4152-52	Altar 84/*A. tauschii* (JBANGOR)	−	1.17**	0.29	+	1.67*	0.29
14	4152-90	Altar 84/*A. tauschii* (502)	−	2.00	0.00	+	2.00*	0.50
15	4154-47	Arlequin	−	3.83	0.29	−	4.33	0.76
16	4152-75	Arlequin/*A. tauschii* (283)	+	2.50*	0.00	−	2.17*	0.29
17	4154-2	Arlequin 1	−	3.25	0.35	−	4.17	0.58
18	4153-4	Arlequin 1/*A. tauschii* (218)	−	1.33*	0.29	+	1.50*	0.00
19	4153-24	Arlequin 1/*A. tauschii* (368)	−	1.17*	0.29	+	2.17*	0.29
20	4153-28	Arlequin 1/*A. tauschii* (335)	−	1.50*	0.50	+	2.17*	0.29
21	4154-35	Botno	+	3.83	1.16	−	4.00	0.50
22	4152-64	Botno/*A. tauschii* (617)	−	2.67	0.29	+	2.67	0.76
23	4152-65	Botno/*A. tauschii* (620)	−	2.67	0.29	+	1.83**	0.29
24	4152-66	Botno/*A. tauschii* (625)	+	2.17	0.29	−	3.17	0.58
25	4154-13	Cerceta	+	3.33	0.58	−	3.67	0.76
26	4152-54	Cerceta/*A. tauschii* (895)	−	1.17*	0.29	−	3.17	0.58
27	4152-85	Cerceta/*A. tauschii* (174)	−	1.67*	0.29	+	1.67*	0.29
28	4152-92	Cerceta/*A. tauschii* (1024)	+	1.67*	0.29	−	2.67	1.00
29	4152-94	Cerceta/*A. tauschii* (1027)	+	1.67*	0.29	−	3.08	0.80
30	4153-12	Cerceta/*A. tauschii* (1025)	+	1.50*	0.00	+	1.83*	0.58
31	4153-14	Cerceta/*A. tauschii* (386)	−	1.17*	0.29	+	1.50*	0.00
32	4153-15	Cerceta/*A. tauschii* (392)	+	1.17*	0.29	−	1.50*	0.00
33	4153-16	Cerceta/*A. tauschii* (533)	+	2.83	0.58	−	4.50	0.00
34	4153-18	Cerceta/*A. tauschii* (1031)	+	2.17	0.76	−	2.17	0.29
35	4153-19	Cerceta/*A. tauschii* (1038)	+	2.17	0.29	+	2.50	1.00
36	4153-20	Cerceta/*A. tauschii* (1046)	+	1.67*	0.29	−	1.83*	0.58
37	4153-21	Cerceta/*A. tauschii* (386)	+	1.67*	0.29	+	2.83	0.58
38	4153-23	Cerceta/*A. tauschii* (368)	+	1.83*	0.29	−	4.17	0.58
39	4153-31	Cerceta/*A. tauschii* (417)	−	2.17	0.58	−	2.17	0.58
40	4154-11	CPI/GEDIZ/3/GOO//JO/CRA	−	3.00	0.50	−	3.67	0.29
41	4152-8	CPI/GEDIZ/3/GOO//JO69/CRA/4/*A. tauschii* (208)	+	1.67*	0.29	−	2.33**	0.29
42	4152-88	CPI/GEDIZ/3/GOO//JO69/CRA/4/*A. tauschii* (409)	−	2.17	0.29	+	1.83**	0.29
43	4153-17	CPI/GEDIZ/3/GOO//JO/CRA/4/*A. tauschii* (1018)	−	3.33	0.29	+	2.33**	0.29
44	4154-1	Croc 1	+	3.00	0.71	−	3.50	1.00
45	4152-6	Croc 1/*A. tauschii* (205)	−	1.17	0.29	+	1.50	0.00
46	4152-24	Croc 1/*A. tauschii* (224)	−	1.00	0.00	+	1.17*	0.29
47	4152-39	Croc 1/*A. tauschii* (725)	−	1.67	0.29	+	1.50	0.00
48	4152-46	Croc 1/*A. tauschii* (879)	−	1.33	0.29	+	1.67	0.29
49	4152-91	Croc 1/*A. tauschii* (517)	−	1.83	0.29	+	1.50	0.00
50	4153-2	Croc 1/*A. tauschii* (210)	+	2.50	1.00	−	3.33	1.26
51	4153-22	Croc 1/*A. tauschii* (212)	−	1.67	0.29	+	2.33	0.29
52	4154-12	D67.2/P66.270	+	4.00	0.50	−	4.17	0.58
53	4152-10	D67.2/P66.270//*A. tauschii* (211)	−	2.50*	0.00	+	1.67**	0.29
54	4152-11	D67.2/P66.270//*A. tauschii* (213)		2.17**	0.29	−	2.33*	0.29
55	4152-13	D67.2/P66.270//*A. tauschii* (217)	−	2.00**	0.50	−	1.50*	0.00
56	4152-15	D67.2/P66.270//*A. tauschii* (218)	−	2.00**	0.50	−	1.50*	0.00
57	4152-18	D67.2/P66.270//*A. tauschii* (220)	+	1.67**	0.29	+	1.83**	0.58
58	4152-21	D67.2/P66.270//*A. tauschii* (221)	−	1.00**	0.00	+	1.33**	0.29
59	4152-22	D67.2/P66.270//*A. tauschii* (222)	+	1.67**	0.29	−	1.83**	0.58
60	4152-23	D67.2/P66.270//*A. tauschii* (223)	+	2.17**	0.29	+	1.83**	0.29
61	4152-56	D67.2/P66.270//*A. tauschii* (257)	seg	1.50*	0.00	+	1.50*	0.00
62	4152-68	D67.2/P66.270//*A. tauschii* (633)	+	2.33*	0.29	+	2.50*	0.00
63	4152-69	D67.2/P66.270//*A. tauschii* (659)	−	2.33*	0.29	+	1.50*	0.00
64	4153-8	D67.2/P66.270//*A. tauschii* (308)	+	2.83*	0.29	−	2.50*	0.00
65	4153-25	D67.2/P66.270//*A. tauschii* (497)	+	2.17*	0.58	−	3.50	1.00
66	4153-26	D67.2/P66.270//*A. tauschii* (1015)	+	1.50*	0.00	−	2.50*	0.00
67	4154-22	Decoy 1	+	3.83	0.29	−	4.33	0.29
68	4152-2	Decoy 1/*A. tauschii* (188)	+	1.33***	0.29	−	2.33**	0.29
69	4152-32	Decoy 1/*A. tauschii* (447)	+	1.83**	0.29	−	2.83**	0.29
70	4152-34	Decoy 1/*A. tauschii* (511)	+	2.33**	0.29	−	2.17***	0.29
71	4152-36	Decoy 1/*A. tauschii* (515)	+	1.67***	0.29	−	1.83***	0.29
72	4152-79	Decoy 1/*A. tauschii* (333)	+	2.50*	0.50	−	4.50	0.00
73	4152-80	Decoy 1/*A. tauschii* (428)	+	2.33**	0.29	−	3.17	0.76
74	4152-83	Decoy 1/*A. tauschii* (458)	+	2.17*	0.58	−	2.50	1.00
75	4152-86	Decoy 1/*A. tauschii* (372)	+	2.17**	0.29	−	2.83*	0.58
76	4152-95	Decoy 1/*A. tauschii* (1030)	+	3.00	0.50	−	4.50	0.50
77	4153-13	Decoy 1/*A. tauschii* (1027)	+	2.50*	0.00	−	3.83	0.76
78	4153-33	Decoy 1/*A. tauschii* (534)	+	2.67	0.76	−	2.50	1.00
79	4154-5	Dverd 2	−	4.50		−	3.67	0.58
80	4152-19	Dverd 2/*A. tauschii* (221)	−	1.00***	0.00	+	1.67*	0.29
81	4152-93	Dverd 2/*A. tauschii* (1027)	+	2.50	0.50	+	4.17	0.58
82	4153-3	Dverd 2/*A. tauschii* (214)	−	1.83*	0.29	+	1.83*	0.29

Continued next page.

Table 1. Continued.

Entry No.†	TA-Line‡	Pedigree	Reaction to ToxA§	Reaction to Ptr		Reaction to *P. nodorum*		
				AVG¶	SD	FLECK#	AVG	SD
83	4154-43	Falcin 1	−	4.33	0.29	−	3.83	1.16
84	4152-76	Falcin/*A. tauschii* (312)	−	1.83***	0.29	+	1.50	0.00
85	4154-26	Gan	−	2.83	1.04	−	4.00	0.50
86	4152-55	Gan/*A. tauschii* (180)	−	1.33	0.29	+	1.50*	0.00
87	4152-61	Gan/*A. tauschii* (408)	−	1.00	0.00	+	1.67**	0.29
88	4152-73	Gan/*A. tauschii* (897)	−	1.33	0.29	+	1.50*	0.00
89	4153-6	Gan/*A. tauschii* (236)	−	1.33	0.29	+	1.83**	0.58
90	4153-27	Gan/*A. tauschii* (206)	−	2.00	0.50	+	2.33*	0.29
91	4153-29	Gan/*A. tauschii* (335)	−	1.33	0.29	−	2.00**	0.50
92	4154-23	GARZA/BOY	−	2.67	0.76	−	3.67	0.29
93	4152-27	GARZA/BOY//*A. tauschii* (311)	−	1.00	0.00	+	1.50**	0.00
94	4154-44	Green 3	−	4.17	0.29	−	4.17	0.58
95	4152-84	Green/*A. tauschii* (458)	−	1.50**	0.00	+	1.67**	0.29
96	4154-37	LCK59.61	+	4.25	0.35	−	4.17	0.76
97	4152-57	LCK59.61/*A. tauschii* (313)	+	1.33*	0.29	−	1.83*	0.29
98	4153-10	LCK59.61/*A. tauschii* (693)	+	1.50**	0.50	−	1.83*	0.58
99	4154-39	Rascon 37	−	2.67	0.58	−	2.67	0.76
100	4152-77	Rascon/*A. tauschii* (312)	−	1.50	0.00	+	1.50	0.00
101	4154-3	ROK/KML	+	3.50	0.00	−	3.67	0.76
102	4152-12	ROK/KML//*A. tauschii* (214)	+	1.67**	0.29	+	2.50	0.00
103	4154-17	Scaup	+	3.83	0.58	−	4.67	0.29
104	4152-62	Scaup/*A. tauschii* (518)	+	1.17**	0.29	+	2.67*	0.76
105	4152-87	Scaup/*A. tauschii* (409)	+	1.83*	0.58	+	2.67	1.61
106	4154-27	Scoop 1	−	2.83	0.58	−	4.33	0.29
107	4152-60	Scoop 1/*A. tauschii* (358)	−	1.00*	0.00	+	2.17*	0.76
108	4154-42	SCOT/MEXI 1	−	3.50	0.50	−	2.00	0.00
109	4152-78	SCOT/MEXI 1//*A. tauschii* (314)	−	1.67**	0.29	+	1.50***	0.00
110	4153-11	SKARV 2/*A. tauschii* (304)	−	1.33	0.29	+	1.50	0.00
111	4154-18	SNIPE/YAV 79//DACK/TEAL	−	3.17	0.76	−	4.17	0.58
112	4152-70	SNIPE/YAV 79//DACK/TEAL/3/*A. tauschii* (700)	−	1.00*	0.00	−	1.17**	0.29
113	4152-72	SNIPE/YAV 79//DACK/TEAL/3/*A. tauschii* (877)	−	1.33*	0.29	−	1.17**	0.58
114	4154-16	Sora	+	4.17	0.29	+	3.33	0.76
115	4152-48	Sora/*A. tauschii* (884)		1.50**	0.00	+	1.50	0.00
116	4153-1	Sora/*A. tauschii* (192)	+	1.33***	0.29	+	1.67*	0.29
117	4153-7	Sora/*A. tauschii* (323)	−	1.67**	0.58	+	1.50	0.00
118	4154-14	Sterna-DW	−	4.17	0.58	+	3.83	1.26
119	4152-59	Sterna-DW/*A. tauschii* (358)	+	1.50*	0.00	+	1.50	0.00
120	4154-28	STY-US/CELTA//PALS/3/SRN 5		3.17	0.29	−	3.00	0.87
121	4153-9	STY-US/CELTA//PALS/3/SRN 5/4/*A. tauschii* (431)	+	2.33*	0.29	+	3.00	0.87
122	4152-89	STY-US/CELTA//PALS/3/SRN 5/4/*A. tauschii* (502)	−	1.00**	0.00	+	1.67	0.29
123	4154-19	TK SN1081	−	4.17	0.29	−	3.50	1.00
124	4153-5	TK SN1081/*A. tauschii* (222)	−	1.17***	0.29	+	1.67	0.29
125	4154-38	Trinakria	−	5.00	0.00	−	3.67	0.29
126	4152-71	Trinakria/*A. tauschii* (700)	−	2.67*	0.58	+	1.83**	0.29
127	4154-31	Yar	+	3.50	0.71	−	3.67	1.26
128	4152-42	Yar/*A. tauschii* (783)	+	1.67	0.29	−	2.17	0.58
129	4152-63	Yar/*A. tauschii* (518)	+	1.17	0.29	+	1.67	0.29
130	4154-21	Yarmuk	+	4.17	0.29	−	4.17	0.58
131	4152-14	Yarmuk/*A. tauschii* (217)	+	2.00**	0.50	−	1.50*	0.00
132	4152-43	Yarmuk/*A. tauschii* (864)	+	1.50**	0.00	+	1.83**	0.29
133	4154-20	YAV 2/TEZ	+	3.75	1.06	−	3.50	1.00
134	4152-53	YAV 2/TEZ//*A. tauschii* (249)	−	1.50	0.00	+	1.50	0.00
135	4152-74	YAV 2/TEZ//*A. tauschii* (895)	−	1.50	0.00	+	1.50	0.00
136	4154-30	YAV 3/SCOT//JO69/CRA/3/YAV 79	−	3.33	0.76	−	3.83	1.16
137	4152-33	YAV 3/SCOT//JO69/CRA/3/YAV 79/4/*A. tauschii* (498)	−	1.33*	0.29	+	1.67	0.29
138	4154-8	68.111/RGB-U//WARD	+	3.17	0.29	−	4.33	0.58
139	4152-37	68.111/RGB-U//WARD/3/*A. taucshii* (629)	−	1.00**	0.00	+	1.50*	0.00
140	4152-28	68.111/RGB-U//WARD/3/*A. tauschii* (316)	+	1.67**	0.29	−	2.00*	0.00
141	4152-29	68.111/RGB-U//WARD/3/*A. tauschii* (326)	+	2.00*	0.50	+	1.67**	0.29
142	4152-82	68.111/RGB-U//WARD/3/*A. tauschii* (454)	seg	1.33*	0.58	+	2.67*	0.76
143	4152-35	68.111/RGB-U//WARD/3/*A. tauschii* (511)	+	1.50**	0.00	+	2.33*	0.29
144	4154-9	68.111/RGB-U//WARD/3/FGO/4/RABI	seg	3.83	0.58	−	4.50	0.00
145	4152-44	68.111/RGB-U//WARD/3/FGO/4/RABI/5/*A. tauschii* (878)	−	1.00*	0.00	+	1.50***	0.00
146	4152-47	68.111/RGB-U//WARD/3/FGO/4/RABI/5/*A. tauschii* (882)	−	2.33*	0.29	+	2.17*	0.58
147	4152-49	68.111/RGB-U//WARD/3/FGO/4/RABI/5/*A. tauschii* (890)	−	1.83*	0.29	−	3.17	0.58
148	4154-7	68.111/RGB-U//WARD RESEL/3/STIL	−	4.17	0.29	−	4.50	0.00
149	4153-30	68.111/RGB-U//WARD RESEL/3/STIL/4/*A. tauschii* (385)	−	2.00**	0.00	−	2.83	1.04
150	4153-32	68.111/RGB-U//WARD RESEL/3/STIL/4/*A. tauschii* (431)	−	2.00**	0.00	−	3.00	0.87
151	4152-40	68.111/RGB-U//WARD RESEL/3/STIL/4/*A. tauschii* (781)	−	1.67***	0.29	−	1.17**	0.29
152	4152-41	68.111/RGB-U//WARD RESEL/3/STIL/4/*A. tauschii* (783)	−	1.67***	0.29	+	1.83**	0.29
153	4154-32	68112/WARD	+	2.67	0.29	−	4.50	0.00
154	4152-30	68112/WARD//*A. tauschii* (369)	+	1.17**	0.29	+	2.33*	0.58
155	4152-31	68112/WARD//*A. tauschii* (369)	+	1.67*	0.29	−	4.17	0.58
156	W-7976	Cando/R143//mexi 'S'/3/*A. tauschii* (C122)	−	1.17	0.29	+	1.83	0.29
157	ND495	Justin*2/3/ND 259/Conley//ND 112	+	4.50	0.00	−	4.33	0.29

* Significantly different from respective durum wheat parents at the 0.05 probability level (*t* test).
** Significantly different from respective durum wheat parents at the 0.01 probability level (*t* test).
*** Significantly different from respective durum wheat parents at the 0.001 probability level (*t* test).
† Entry number: The assigned number in this study.
‡ TA-Line: The TA number and line number used in Wheat Genetics Resource Center (WGRC) at Kansas State University in Manhattan, KS. At WGRC, TA4152, TA4153, and TA4154 are used to represent Elite 1, Elite 2, and durum wheat parents, respectively (Jon Raupp, 2002, personal communication).
§ Reaction to Ptr ToxA: Insensitive (−), sensitive (+), and segregation (seg).
¶ With reactions to *P. tritici-repentis* and *P. nodorum*, AVG = average reaction of each genotype (three replications).
# FLECK = necrotic flecking: The genotypes had no flecking (−) or showed flecking (+) in at least one replication.
†† *Aegilops tauschii* Coss. accession number in CIMMYT Wheat Wide Crosses working collection.

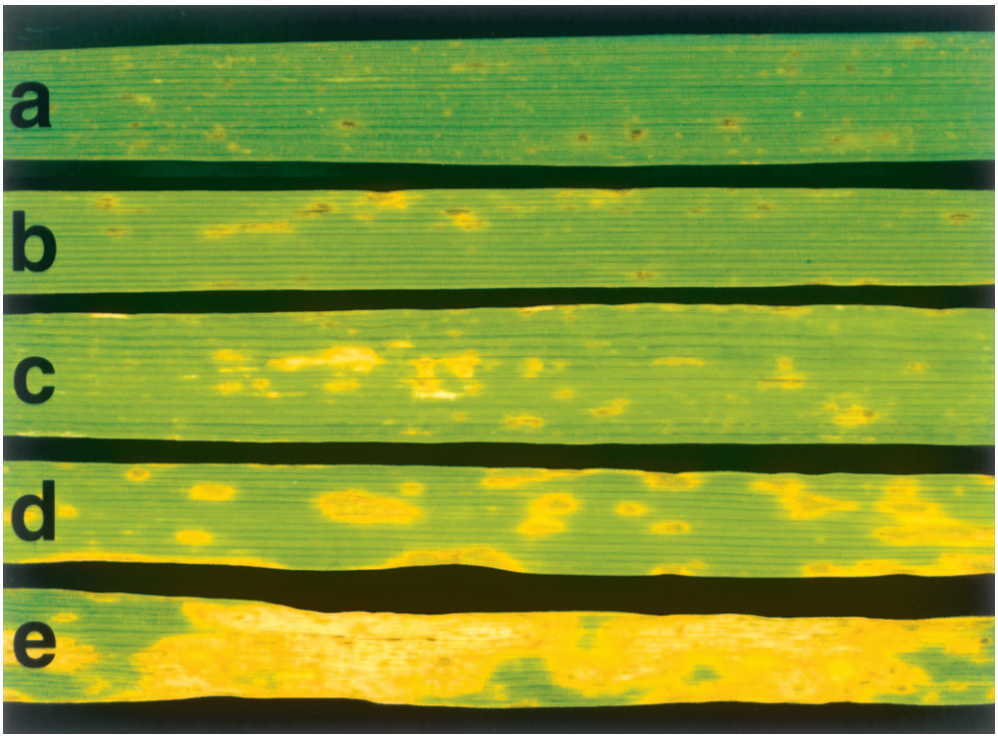

Fig. 1. Photograph of reaction (lesion) types induced by Sn2000 of *Phaeosphaeria nodorum* in synthetic hexaploid wheat (SHW) and hard red spring wheat (HRSW). (a) Type 1: Penetration points with flecking and/or small dark spots in SHW line TA4152-1 (resistant); (b) Type 2: Lesions with dark spots and little surrounding necrosis/chlorosis in SHW line TA4152-11 (moderately resistant); (c) Type 3: Dark lesions (2–3 mm in size) completely surrounded by necrosis or chlorosis in SHW line TA4152-66 (moderately susceptible); (d) Type 4: Larger necrotic or chlorotic lesions (4 mm or greater in size) with little coalescence in HRSW line ND495 (susceptible); (e) Type 5: Large coalescing lesions with very little green tissue remaining in SHW line TA4152-79 (highly susceptible).

ble) (Fig. 1d); Type 5 consists of large coalescing lesions with very little green tissue remaining (highly susceptible) (Fig. 1e).

In addition to the different types of lesions, *P. nodorum* caused necrotic flecking in some genotypes. We rated a genotype as necrotic flecking (+) when the plant leaves showed apparent tiny necrotic or chlorotic flecks in contrast to the plants without flecks (−) (Fig. 2).

Statistical Analysis

Statistical analysis was performed using the Statistical Analysis System version 8.2 (SAS Institute, 1999). The two sample *t* test was used to test the difference of average reactions to *P. tritici-repentis* and *P. nodorum* between each of the synthetics and its respective durum parent. Simple linear regression analysis was performed to evaluate the association of sensitivity to Ptr ToxA with average reaction to *P. tritici-repentis* and the association of necrotic flecking with average reaction to *P. nodorum*.

RESULTS AND DISCUSSION

A total of 155 entries, including 120 elite CIMMYT synthetics and 35 durum wheat genotypes used as the parents of the synthetics, were evaluated for seedling reactions to *P. tritici-repentis*, Ptr ToxA, and *P. nodorum*. The evaluation data are shown in Table 1 and the average reactions to *P. tritici-repentis* and *P. nodorum* and standard deviations were calculated from three replications for all the synthetics and the majority of durum parents.

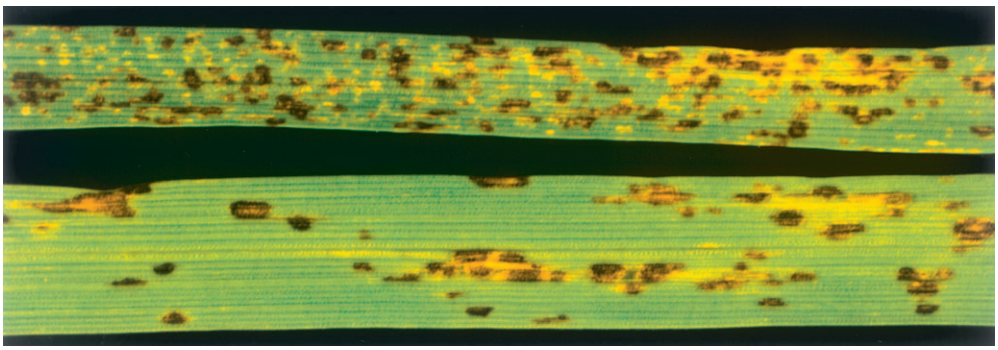

Fig. 2. Necrotic flecking induced by Sn2000 of *Phaeosphaeria nodorum* in synthetic hexaploid wheats. The upper leaf shows a genotype with tiny necrotic points or flecks in comparison with a genotype (lower leaf) without chlorotic or necrotic flecks.

Sensitivity to Ptr ToxA

The proteinaceous Ptr ToxA is a 13.2-kDa HST that causes necrosis on the leaves of sensitive genotypes of wheat (Ciuffetti and Tuori, 1999). The sensitivity to Ptr ToxA is controlled by the dominant gene *Tsn1* on the long arm of wheat chromosome 5B (Faris et al., 1996). The genotypes without *Tsn1* are insensitive to the toxin (Anderson et al., 1999). Most synthetics, as expected, were the same as their durum wheat parents in their reaction to Ptr ToxA. For example, durum wheats 'Aconchi 89' (Entry 1), 'Altar 84' (Entry 3), 'Arlequin 1' (Entry 17), 'Falcin 1' (Entry 83), 'Gan' (Entry 85), 'Rascon 37' (Entry 99), 'Scoop 1' (Entry 106), TK SN1081 (Entry 123), and 'Trinakria' (Entry 125) were insensitive (Table 1), and all the synthetics with these durum parents were also insensitive. Durum wheats 'Decoy 1' (Entry 67), LCK59.61 (Entry 96), 'Scaup' (Entry 103), and 'Yarmuk' (Entry 130) were sensitive, and the synthetics with these durum parents were all sensitive.

Some synthetics derived from the crosses with durum wheats Botno (Entry 21), 'Cerceta' (Entry 25), 'Deverd 2' (Entry 79), and some F_1 hybrids of two durum varieties (Entries 52 and 133), or the progenies of multiway crosses involving three to five durum genotypes (entries 40 and 138) showed different reactions to Ptr ToxA from their durum parents. And, durum wheat 'Croc 1' (Entry 44) was sensitive (+), but only one (Entry 50) of seven synthetics with Croc 1 was sensitive (Table 1). The differences could be caused by the heterozygosity of the sensitivity loci and heterogeneity of the durum parents, heterogeneity of synthetics, or the existence of a sensitivity locus on D-genome chromosomes. The durum parents of a number of synthetics were the F_1 hybrids of two durum genotypes or the progenies of multiway crosses involving three to five durum genotypes (Mujeeb-Kazi et al., 2000, Mujeeb-Kazi and Delgado, 2001). Therefore, if the durum varieties had different reactions to Ptr ToxA, and their immediate hybrids were used as the parents of the synthetics, then the sensitivity and insensitivity would segregate among the synthetics. Most noticeably, the synthetics derived from multi-way crosses such as CPI/GEDIZ/3/GOO//JO69/CRA/4/*A. tauschii* (Entries 41–43), D67.2/P66.270//*A. tauschii* (Entries 53–66), STY-US/CELTA//PALS/3/SRN 5/4/*A. tauschii* (Entries 121 and 122), and 68.111/RGB-U//WARD/3/*A. tauschii* (entries 139–143) had different reactions (Table 1). In these synthetics, the durum parents tested in this study may have advanced a number of generations since they were used as the parents of the synthetics.

Reactions to *Pyrenophora tritici-repentis*

The 120 synthetics had average disease reactions to *P. tritici-repentis* ranging from 1.00 to 3.33, with an overall average of 1.70, while the 35 durum parents had average disease reactions ranging from 2.67 to 5.00, with an overall average of 3.61 (Table 1). Fifteen (12.50%) of 120 synthetics had an average reaction of 1.00, and 26 (21.67%) had a similar reaction (1.17–1.33) to the resistant check W-7976 (1.17) (Table 1). Thus, 41 (34.17%) synthetics showed Type 1 (resistant) reaction mode. In addition, 15 (12.50%) synthetics had an average reaction of 1.50, and 50 (41.67%) had a Type 2 (moderately resistant) reaction mode. These results suggest that the elite CIMMYT synthetics are an excellent source of resistance to tan spot. Contrary to the synthetics, the durum wheat parents did not exhibit Type 1 or 2 reactions, suggesting that a good level of resistance does not exist in these durum wheat genotypes. Fourteen (40.00%) of 35 durum wheat genotypes had a reaction mode of 3.00 (moderately resistant or moderately susceptible) and the remaining lines had reaction modes of 3.50 or greater.

Table 2. Coefficient of determination values (R^2) showing associations of sensitivity to Ptr ToxA vs. average reaction to *Pyrenophora tritici-repentis* (Ptr), necrotic flecking vs. average reaction to *Phaeosphaeria nodorum* (Pn).

	R^2	
Traits	**Synthetic wheat**	**Durum wheat**
ToxA sensitivity, reaction to Ptr	**0.1159*****	**0.0018**
Necrotic flecking, reaction to Pn	**0.2044*****	**0.0172**

***** Significant at the 0.001 probability level.**

Resistance genes for tan spot have not been located on D-genome chromosomes in hexaploid wheat. However, resistance has been found in some *A. tauschii* accessions (Siedler et al., 1994). We observed that all five synthetics of different durum genotypes with *A. tauschii* accessions 221 (Entries 11, 58, and 80) and 224 (Entries 12 and 46) showed average reactions of 1.00, suggesting that these *A. tauschii* accessions may possess resistance genes to the tan spot fungus. Thus, further studies are needed to confirm the resistance from *A. tauschii* by evaluating the resistance of *A. tauschii* accessions used as the parents of elite CIMMYT synthetics.

Host sensitivity to Ptr ToxA has been found to be associated with disease susceptibility to *P. tritici-repentis* race 2 (Friesen et al., 2003a, Lamari and Bernier, 1991). Simple linear regression analysis in this study indicated that the sensitivity to Ptr ToxA was associated with disease susceptibility to race 1 in the synthetics (Table 2; $R^2 = 0.1159$, $P < 0.001$) but not in their durum parents. This preliminary observation suggests that the insensitivity to the toxin contributed to the enhanced resistance in some synthetics to a certain extent. Nevertheless, it appears that resistance genes and gene interactions play a major role in enhancing the resistance in the synthetics because most of the sensitive synthetics exhibited significantly higher resistance than their sensitive durum parents (Table 1). The highest level of resistance in the synthetics was probably contributed from mutual actions of resistant genes and insensitivity to the toxin. We observed that all 17 synthetics with an average reaction of 1.00 were insensitive (Table 1). This knowledge will be useful in developing new resistant germplasm and cultivars. To best defend the crop from tan spot, both insensitivity to the toxin and other resistance genes need to be incorporated into bread wheat cultivars.

Reaction to *Phaeosphaeria nodorum*

The 120 synthetics had average reactions to *P. nodorum* from 1.17 to 4.5, with an overall average of 2.11,

while the 35 durum lines had average reactions from 2.00 to 4.67, with an overall average of 3.85 (Table 1). Among 120 synthetics, 9 (7.50%), 28 (23.33%), and 50 (41.67%) lines had reaction modes of 1.00 (resistant), 1.50 (resistant or moderately resistant), and 2.00 (moderately resistant), respectively. However, only one (Entry 108) of 35 durum genotypes had an average reaction of 2.00, and the remaining 34 genotypes had reaction modes of 3.00 or greater (Table 1). Because most of the durum wheat genotypes in this study were susceptible, the high level of resistance in the synthetics is most likely contributed by the resistance gene(s) in the D-genome chromosomes from *A. tauschii* or intergenomic gene interactions. The resistance to *P. nodorum* controlled by a single gene was identified in *A. tauschii* (Murphy et al., 2000).

Different from the reactions to *P. tritici-repentis*, *P. nodorum* caused apparent chlorotic, necrotic flecking in addition to the different types of lesions in some synthetics and durum genotypes (Fig. 2). Among 120 synthetics, except for 44 (36.67%) lines without flecking (−), 76 (63.33%) lines showed flecking in at least one of three replications. Simple linear regression analysis indicated that necrotic flecking was associated with the level of resistance in the synthetics (Table 2; $R^2 = 0.2044$, $P < 0.001$).

The evaluation data reported in this study represent a preliminary observation on the resistance of elite CIMMYT synthetics to *P. tritici-repentis* and *P. nodorum*. Additional study is needed to verify the resistance. A 2-yr and two-location experiment to evaluate adult-plant resistance of these synthetics is currently underway. The evaluation data in this study showed that 26 synthetics (4152-1, 4152-3, 4152-5, 4152-6, 4152-7, 4152-9, 4152-20, 4152-21, 4152-24, 4152-25, 4152-27, 4152-37, 4152-44, 4152-48, 4152-53, 4152-55, 4152-56, 4152-59, 4152-70, 4152-73, 4152-74, 4152-77, 4153-4, 4153-11, 4153-14, and 4153-15) had high levels of resistance to both tan spot and SNB (Table 1). The evaluation data from other studies (Mujeeb-Kazi et al., 2000; Mujeeb-Kazi and Delgado, 2001) indicated that all of the 26 synthetics were resistant to stripe rust, 21 were resistant to Karnal bunt, 20 were resistant to Septoria tritici leaf blotch, and five (4152-24, 4152-37, 4152-44, 4152-48, and 4152-55) were resistant to FHB. These synthetics can be used for developing new adapted germplasm with resistance to multiple diseases. Also, some of these synthetics should be excellent parental lines for developing mapping populations.

In conclusion, 120 elite CIMMYT synthetics and their durum wheat parents were evaluated for seedling resistance to tan spot and SNB. A number of synthetics with high levels of resistance to the two foliar diseases have been identified, and they represent a potential new source of resistance. Because these synthetics have been widely distributed and are considered building blocks of the germplasm base in hexaploid wheats, the data from this study provide additional guidance in selecting parental lines for development of new resistant cultivars and mapping populations. The synthetics with multiple disease resistances would be excellent parental germplasm for developing mapping populations for multiple purposes.

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REFERENCES

Ali, S., and L.J. Francl. 2003. Population race structure of *Pyrenophora tritici-repentis* prevalent on wheat and noncereal grasses in the Great Plains. Plant Dis. 87:418–422.

Anderson, J.A., R.J. Effertz, J.D. Faris, L.J. Francl, S.W. Meinhardt, and B.S. Gill. 1999. Genetic analysis of sensitivity to a *Pyrenophora tritici-repentis* necrosis-inducing toxin in durum and common wheat. Phytopathology 89:293–297.

Ciuffetti, L.M., and R.P. Tuori. 1999. Advances in the characterization of the *Pyrenophora tritici-repentis*–wheat interaction. Phytopathology 89:444–449.

Cox, T.S. 1998. Deepening the wheat gene pool. J. Crop Prod. 1:1–25.

Eyal, Z. 1999. Breeding for resistance to *Septoria* and *Stagonospora* disease of wheat. p. 332–344. *In* J.A. Lucas et al. (ed.) *Septoria* on cereals—A study of pathosystems. IACR-Long Ashton Research Station, Bristol, UK.

Faris, J.D., J.A. Anderson, L.J. Francl, and J.G. Jordahl. 1996. Chromosomal location of a gene conditioning insensitivity in wheat to a necrosis-inducing culture filtrate from *Pyrenophora tritici-repentis.* Phytopathology 86:459–463.

Fried, P.M., and E. Meister. 1987. Inheritance of leaf and head resistance of winter wheat to *Septoria nodorum* in a diallel cross. Phytopathology 77:1371–1375.

Friesen, T.L., S. Ali, S. Kianian, L.J. Francl, and J.B. Rasmussen. 2003a. Role of host sensitivity to Ptr ToxA in development of tan spot of wheat. Phytopathology 93:397–401.

Friesen, T.L., S.S. Xu, J.D. Faris, J.B. Rasmussen, J.D. Miller, and M.O. Harris. 2003b. Evaluation of Langdon durum-*Aegilops tauschii* synthetic hexaploid wheats for reaction to tan spot, Stagonospora leaf blotch, leaf rust, stem rust, and Hessian fly. p. 1133–1135. *In* N.E. Pogna et al. (ed.) Proc. 10th Int. Wheat Genet. Symp., Pasetum, Italy. 1–6 Sept. 2003. Istituto Sperimentale per la Cerealicoltura, Rome.

King, J.E., R.J. Cook, and S.C. Melville. 1983. A review of *Septoria* diseases of wheat and barley. Ann. Appl. Biol. 103:345–373.

Lamari, L., and C.C. Bernier. 1989. Evaluation of wheat lines and cultivars to tan spot [*Pyrenophora tritici-repentis*] based on lesion type. Can. J. Plant Pathol. 11:49–56.

Lamari, L., and C.C. Bernier. 1991. Genetics of tan necrosis and extensive chlorosis in tan spot of wheat caused by *Pyrenophora tritici-repentis.* Phytopathology 81:1092–1095.

Lamari, L., S.E. Strelkov, A. Yahyaoui, J. Orabi, and R.B. Smith. 2003. The identification of two new races of *Pyrenophora tritici-repentis* from the host center of diversity confirms a one-to-one relationship in tan spot of wheat. Phytopathology 93:391–396.

Liu, Z.H., T.L. Friesen, J.D. Faris, S. Meinhardt, S. Ali, and J.B. Rasmussen. 2003. Mapping of wheat sensitivity to a partially purified host-selective toxin produced by *Stagonospora nodorum*. p. 139–141. *In* G.H.J. Kema et al. (ed.) Global Insights Into the Septoria and Stagonospora Diseases of Cereals. Proc. of the 6th Int. Symp. on Septoria and Stagonospora Diseases of Cereals, Tunis, Tunisia. 8–12 Dec. 2003. Publ. in Tunisia.

McFadden, E.S., and E.R. Sears. 1944. The artificial synthesis of *Triticum spelta.* Genetics (The Hague) 30:14.

McKendry, A.L., G.E. Henke, and P.L. Finney. 1995. Effects of Septoria leaf blotch on soft red winter wheat milling and baking quality. Cereal Chem. 72:142–146.

Mujeeb-Kazi, A., and R. Delgado. 2001. A second, elite set of synthetic hexaploid wheats based upon multiple disease resistance. Ann. Wheat Newsl. 47:114–116.

Mujeeb-Kazi, A., G. Fuentes-Davila, R. Delgado, V. Rosas, S. Cano, A. Cortés, L. Juarez, and J. Sanchez. 2000. Current status of D-genome based, synthetic, hexaploid wheats and the characterization of an elite subset. Ann. Wheat Newsl. 46:76–79.

Murphy, N.E.A., R. Loughman, R. Wilson, E.S. Lagudah, R. Appels, and M.G.K. Jones. 2000. Resistance to Septoria nodorum blotch in the *Aegilops tauschii* accesion RL 5271 is controlled by a single gene. Euphytica 113:227–233.

Rees, R.G., and G.J. Platz. 1983. Effects of yellow spot on wheat: Comparison of epidemics at different stages of crop development. Aust. J. Agric. Res. 34:39–46.

Rees, R.G., and G.J. Platz. 1990. Sources of resistance to *Pyrenophora tritici-repentis* in bread wheats. Euphytica 45:59–69.

Riede, C.R., L.J. Francl, J.A. Anderson, J.G. Jordahl, and S.W. Meinhardt. 1996. Additional source of resistance to tan spot of wheat. Crop Sci. 36:771–777.

SAS Institute. 1999. SAS/STAT user's guide. Releases 8.2, 8.1, 8.0. SAS Inst., Cary, NC.

Siedler, H., A. Obst, S.L.K. Hsam, and F.J. Zeller. 1994. Evaluation for resistance to *Pyrenophora tritici-repentis* in *Aegilops tauschii* Coss. and synthetic hexaploid wheat amphiploids. Genet. Res. Crop Evol. 41:27–34.

Zhang, H.-F., L.J. Francl, J.G. Jordahl, and S.W. Meinhardt. 1997. Structural and physical properties of a necrosis-inducing toxin from *Pyrenophora tritici-repentis.* Phytopathology 87:154–160.